and no siphonoglyphe. 5th. The Alcyonidæ, a large and somewhat heterogeneous group containing all the remaining genera of the Alcyonaria, which, though exhibiting many wide variations, *inter se*, agree in possessing no specially marked characters of deviation from an ideal central form from which, I suppose, they must have sprung.

IV. "On the Variations of Latency in certain Skeletal Muscles of some different Animals." By THEODORE CASH, M.D. and GERALD F. YEO, M.D. Communicated by Dr. SANDERSON, F.R.S. Received May 29, 1883.

In a former paper ("Proc. Roy. Soc.," vol. 33, p. 462) we laid before the Society the results of a series of experiments by which we had endeavoured to ascertain accurately the differences in the duration of the latent period of contraction of skeletal muscle (frog's gastrocnemius) which could be brought about by varying the following influences:—

1. The weight of load.
2. The mode of applying weight (supported or unsupported).
3. The strength of stimulation.
4. Temperature.
5. Fatigue.

We have since been engaged in determining the relative duration of the latent periods of different skeletal muscles of vertebrate animals. Besides several muscles of the *Rana temp.*, we have examined some from the toad, tortoise, small mammals, and birds. In this paper, which is intended to be a continuation of the one above referred to, we beg leave to lay before the Society the results of these experiments and our general conclusions.

We know from the works of Fick,* Marey,† Ranvier,‡ Frédéricq,§ Richet,|| and one of us,¶ that various muscles in the same animal have a mode of contraction differing more or less from one another, and adapted to the kind of work they have to perform. But in the works of most of these authors little information can be found concerning the variations in the duration of the latent period, in differently contracting muscles, whether those of the same animal or those of different animals.

* Fick, "Irritabelen Substanzen."

† Marey, "Du Mouvements dans les Fonctions de la Vie."

‡ Ranvier, "Leçons sur le Système Musculaire."

§ Frédéricq, "Bull. de l'Acad. roy. de Belgique," lvii, No. 6.

|| Richet, "Physiologie des Muscles," &c.

¶ Cash, "Journal of Anat. and Phys.," vol. xv.

As our desire was to obtain information of the latency actually occurring in the muscle, we adopted the same plan in this series as in our former experiments of stimulating the muscle directly. The whole length of the muscle was introduced into the secondary circuit, and a contraction registered, resulting from a maximal opening shock of Du Bois Reymond's inductorium with a single pint Daniell cell. The arrangement of the apparatus was similar to that employed in our former series of experiments.

We shall tabulate the mean results of a series of measurements of curves obtained from a number of observations upon the animals above mentioned, and we believe they will prove, that while the latencies for different muscles of the same animal bear amongst themselves certain proportion to the length of their succeeding curves, we can by no means reason from one group of animals to another what this relationship may be.

Though the duration of the latency of each individual muscle varies within certain limits in different frogs, we think we can vouch for the correctness of the inter-relationship of the results furnished by the various muscles employed in arriving at the averages given. Our measurements confirm with considerable exactitude those obtained by one of us from experiments made with the muscles of *Rana esculenta*,* in which another method was employed. We have naturally regarded those results as most satisfactory, in which, by working rapidly, we succeeded in obtaining representative curves of the whole series of muscles furnished by one animal.

Frog.

Table I.

Rana Temporaria.—Examined in December. The average of the measurements obtained from a large number of experiments is given.

Muscle.	Weight.	Length of latency.	Altitude.	Length of curve.
Gastrocnemius ..	10 grms.	·0117″	23 mm.	·12″
Triceps	10 "	·0114″	30 "	·112″
Semimembranosus	10 "	·0116″	28 "	·119″
Hyoglossus......	5 "	·015″	29 "	·18″
Rectus abd......	5 "	·014″	33 "	·167″
Biceps crur......	5 "	·0124″	18·5 "	·12″

* Cash, "Journal of Anat. and Phys.," vol. xv.

Toad.

Table II.

The averages of several experiments made during December and January. Fresh specimens which as a rule had been but one night in captivity were examined. (The weather having been very mild during the time of experimentation the animals were active and vigorous.)

Muscle.	Weight.		Length of latency.
Gastrocnemius..	10 grms.	....	·0123″
Triceps	10 "	....	·0121″
Hyoglossus	6 "	....	·0191″
Rectus abd.	6 "	....	·0191″
Biceps crur.	6 "	....	·0135″
Sartorius	6 "	....	·015″

March.—From perfectly fresh *Toads* the following variations in values were obtained. The animals had not spawned :—

Muscle.	Variation of length of latency.		
Gastrocnemius	·0135″	....	·0146″
Triceps	·0128″	....	·0128″
Hyoglossus	·015″	....	·0192″
Rectus abd.	·013″	....	·015″
Biceps crur.	·015″	....	·0155″
Sartorius	·0137″	....	·0146″

The durations of the latencies in the latter part of Table II differ but slightly from those obtained from the "winter frog," as will be seen from contrasting the following muscles :—

Muscle.	(Fresh) Toad (March.)		Frog (December).
Gastrocnemius	·0135″	....	·0117″
Triceps............	·0128″	....	·0114″
Hyoglossus	·015″	....	·015″
Biceps crur.........	·015″	....	·0124″
Rectus abd.	·013″	....	·014″

It is worthy of note that the more pronounced differences of latency between toad and frog lie in the muscles of the extremities; the trunk muscles yield more nearly equal values. An appeal to function shows that the circumstance is highly probable. The frog which depends upon speed of movement for procuring its food, for safety from enemies, and preservation from death in times of drought, has different motor requirements from the toad, which depends for safety

on crouching, and on its approximation of colour to that of surrounding objects, whilst it rather waits for its food to come to it, than attempts to pursue it. But the requirements of the trunk muscles are much more similar in the two animals, and thus we find the hyoglossus for procuring food, and the rec. abdominis for spawning, respiration and flexion of the body, yielding very similar values.

Tortoise.

In order to obtain a complete record of the long curve of contraction of the tortoise muscle, and at the same time an exact estimation of its latency, a second recording surface had to be employed. The apparatus was therefore so arranged that the tendon of the muscle drew upon the membrane of a Marey's tambour, which acted as a weight beneath the lever which recorded on the plate of the pendulum. By means of a second inverted tambour armed with a light lever, the transmitted movement was written on a rotating cylinder. The commencement of the curve including the time of latency, was drawn on the rapidly moving plate of the pendulum, and simultaneously a graphic record of the shape and duration of the total curve was obtained on the drum. The results could be associated after measurement of the tuning-fork curves, by means of which the time was in each case controlled.

Tortoise.

Table III.

Muscles of Land Tortoise. Examined in Winter.

The muscles were prepared as rapidly as possible with their bony insertions or attachments to the carapace preserved. Stimulation direct maximal.

Muscle.*	Weight.	Latency.	Length of curve to notch.	Length of curve to abscissa (circa).
Omohyoid	30 grms.	·0225″	·83″	4″—6″
Semimembranosus	30 ,,	·0247″	1″	4″
Biceps fem.	10 ,,	·028″	1·16″	5″
Ext. dig. com. ..	10 ,,	·033″	1·3″	5·5″

Of these muscles the first two are strictly parallel fibred. The omohyoid is the agent chiefly concerned in the retraction of the head,

* For nomenclature of muscles, see Bojanus, "Anatome Testudinis Europææ," Vilnæ, 1849.

the most rapid movement of which the animal is capable. The semi-membranosus passes over three joints, and a considerable extent of contraction is necessary in order to enable it to flex the foot on the knee, and the thigh on the pelvis. Both of these muscles arrive speedily at a maximum of contraction, ·18″ and ·24″, and coincidently with this rapid action we have the relatively short latency quoted. There is a considerable difficulty in estimating the length of curve of the tortoise muscle, owing to its gradual return to the base line. Usually a notch in the descending part of the curve shows the distinction between the active curve and the after shortening which is so marked a feature in the action of the muscles of this animal; but occasionally the one passes into the other by insensible gradations. We have, however, endeavoured by varying the burden to produce some indication of this notch when none at first existed, and we have confined ourselves to the results which we believe to be correct.

Warm-blooded Animals.

The muscles of warm-blooded animals were examined *in situ*, the circulation being as little as possible interfered with, and the animal kept well under the influence of anæsthetics. A modification of Ranvier's rabbit-holder was utilized in order to support the animal in the necessary relationship to the recording lever. The head-holder at one end of a small board, consisted of a loop of metal covered with cord, which received the snout or beak and anterior part of the head, whilst a piece of string run through two openings in the loop, and behind the occiput kept the head in position, and facilitated the administration of ether. The board which served to support the animal was perforated with numerous holes, through which strings attached to the animal passed. The under surface of the board was fitted with a ball and socket joint, which could be clamped firmly to the sliding table on which the lever rested. By a screw which fixed the cup around the ball, this joint could be tightened when the board was adjusted to any given position, and thus the muscle to be examined could be brought into direct line of traction with the lever without altering the attachment of the animal or otherwise disturbing the apparatus. The axis of the lever was provided with a short arm projecting on the side opposite to the lever, to which a thread passing from the muscle was attached. The arm was drawn downwards by the contracting muscle, and the lever therefore upwards, so that a curve in every way comparable to those obtained by direct traction was drawn.

Mammals.

Table IV.—Adult Rat.

The gastrocnemius of the rat draws a curve with a double summit.

The value of the curve to the first distinct fall of the lever is ·13″, but relaxation occurs slowly after this.

Muscle.	Weight.	Latency.	Length of curve.
Gastrocnemius ..	30 grms.	·011″	·13″

The maximum of contraction is reached in about ·03″.

Table V.—Kitten (two months old).

Muscle.	Weight.	Latency.
Gastrocnemius	30 grms.	·018″

Birds.

The muscles of three birds were examined.

Table VI.

Animal.	Muscle.	Weight.	Latency.	Length of curve.
Hen........	Gastrocnemius ..	30 grms.	·0204″	·116″
Pigeon......	"	30 "	·012″	·074″
	Pect. maj.........	30 "	·011″	·083″
Blackbird ..	Gastrocnemius ..	..	·0125″	·081″
	Biceps brach......	..	·014″	·087″
Max. of biceps brach. ·045″.				

We will not recapitulate the results given in the tables further than by drawing attention to the extremes of the values obtained. In the December frog we found the triceps directly stimulated had the shortest latency (·0114″), whilst the hyoglossus had the longest ·015″. The muscles of the trunk hyoglossus and rectus abdominis (compound but parallel fibred muscle) exhibited longer latencies than did the muscles of the extremities; the muscles of the arm again longer than those of the leg.

In forming our conclusions concerning the duration of the latent period of contraction of skeletal muscles, and the variations it is subject to, we must refer repeatedly to our former paper, of which this, as has been said, may be regarded as the continuation.

The latencies of gastrocnemii of *Rana temp.*, examined between January and April, and selected at random, varied between wide limits, namely from ·008″—·0208″. These values include also measurements taken from curarised gastrocnemii, but as we have already pointed out, the small dose of curare employed appeared in no way to cause any divergence in reaction of the muscle from the normal. In this respect our results confirm the view expressed by Pflüger. In

support of this we may mention that the shortest latency referred to occurred in a curarised, the longest in a non-curarised muscle. In the case of the toad, variations due solely to the individual were considerable, but the divergencies were not so great as in the case of the frog. Thus in six gastrocnemii taken from different individuals the range was from ·0125″ to ·017″, in the triceps (six muscles) from ·012″ to ·015″, and in the hyoglossus ·015″ to ·024″. We seldom found any material difference in the latencies of corresponding muscles in the same animal. The toads examined in December and January yielded latencies averaging ·0121″ (triceps) and ·0191″ (hyoglossus and rectus abdom.), whilst the March animals gave ·0128″ (triceps) as the shortest, and ·015″ (hyoglossus and biceps) as the longest latencies. The subjects of the latter experiments were unspawned animals, and the reaction of the trunk muscles was marked by an accession of irritability.

In the tortoise, the long parallel fibred muscles, omohyoid and semibranosus, yielded the shortest latencies, viz., ·0225″ and ·0247″ respectively, whilst the wide bellied biceps and the broad but short extensor communis digitorum gave distinctly longer periods (·028″ and ·033″). The gastrocnemius of a kitten, aged two months, showed a latency of ·018″, and that of a white tame rat ·011″.

In the pigeon the pectoralis major has a slightly shorter latency (·01″) than the gastrocnemius, but in the blackbird the biceps (a muscle intimately connected, as is the pectoralis, with flying movements) appears to have a latency longer by ·0015″ than the gastrocnemius of the same bird. It is worthy of remark, however, that the blackbird had been reared and kept in confinement, and therefore it is probable that the muscles connected with flight were to a certain extent uneducated and undeveloped.

To sum up the variations in latency obtained between the frog muscle, which, free from exceptional influences, yielded the shortest (·008″), and the tortoise muscle, which yielded the longest (·033″), we have but a range through ·025″, a variation small enough to be in itself surprising, but still more so when we consider the relative durations of the contractions to which these latencies are initial. We may certainly infer from these results that, though the intralatent processes in the various muscles of a given animal have a certain inter-relationship with the resulting contractions, and that each muscle variety gives divergencies from its normal latency and contraction only within certain limits, that we can establish no argument of probabilities from an animal of one species to an animal of another species as regards the latency preceding contraction. The same holds true of warm-blooded as well as of cold-blooded, of Carnivora as of Rodentia.

The literature published during the last twenty years relating to the duration of the latent period, bears witness to the very different lines

of investigation pursued by experimenters, as well as to the widely varying results which they have obtained. It seemed to us, therefore, that time devoted to a systematic examination with one exact method of the many aspects of the subject would be advantageously employed, and would furnish results relatively correct, and of a value which would be greater than could be obtained by grouping the conclusions of numerous authors, whose methods and objects of research differed and who had no unanimous starting point for their investigations.

For the gastrocnemius of a frog:
Helmholz* gives as a latency.................... ·01″
Place† and Gad‡ .... ·004″

whilst Mendelssohn,§ who has admirably grouped the results obtained by these and other authors, found that in frogs taken at random of various sizes and in different seasons, the latency varied within the wide limits of ·004″—012″. Navalachin‖, who has ably investigated the production of heat during the active contraction of striated muscle, has pointed out that the latency of the frog's gastrocnemius is shorter in the spring than in the summer months. Here we have to do with another element rather than with temperature—namely, with the spawning of the animal, the most disturbing internal influence to which a frog is liable. The latencies before and after spawning are various, the irritability of the muscles being different. This is in its effect almost convertible with the experience of Helmholz, Engelmann, Lautenbach, and others,¶ who have pointed out that increase in strength of stimulation shortens the latency. In the spring-time the irritability of the animal is increased, and maximal stimulation, which in the summer frog would produce a certain definite effect, is here hyper-maximal (so to speak) and the latency is correspondingly shortened. To the same reason, *i.e.*, an increase in irritability, Mendelssohn looks for the explanation of the shortened latency of the muscle, whose nerve has just been divided. We must, however, confess that we are unable to confirm his results, *i.e.*, that the latency in the case of the muscle of which the nerve has just been divided, may be temporarily shortened by half, in the case of the *Rana temp.* The latency given by Gad (·004″) associated with a lengthening of the muscle as precursor to its general contraction, we cannot attempt to criticise, as we have very rarely ourselves seen the form of curve he represents as being normal, but which he only

* Helmholz, "Müller's Archiv," 1850.

† Place, "Nederland Archiv v. Genees. en Natuur," III, 1867.

‡ Gad, "Ueber das Latenzstadium, &c.," "Archiv f. Anat. und Phys.," 1879.

§ Mendelssohn, "Marey's Travaux," 1878-9.

‖ Navalachin, "Myothermische Untersuchungen," "Pflüger's Arch.," Bd. XIV.

¶ See Tables IV and V in former paper.

obtained where the muscle is transfixed by the lever. An intra-latent lengthening of the entire muscle does occasionally occur, but in our experiments it had no constant relationship whatever to the time of stimulation, and we therefore regarded it as a chance extension. We have not, however, been able to find time to repeat the experiments—using his methods—from which Gad deduces his results.

The brief latency that Place and Klunder obtained from stimulation of the already shortening muscle, we have rarely seen. When it does occur, its accurate estimation becomes extremely difficult, as it is necessary to separate the moment when active contraction commences from the passive shortening which preceded it, and one phase often passes into the other by almost insensible gradations. Fallacies of so extensive a nature arise from the use of a slowly moving recording surface, and of a short lever, that we have in all cases employed a rapid swing of the pendulum myograph, and a lever multiplying the contraction by six or seven times, for the production of the curves from which our data of latencies are taken. In the fatigued muscle, for instance, commencing contraction is very gradual; so gradual in fact that its earlier phases may, with a short lever, be readily mistaken for a prolongation of the latency. We need not point out that with a comparatively slowly moving cylinder slight inaccuracies in measurement—at all times subject to occur—are multiplied proportionally as the speed becomes slower.

A cursory examination of the tables in our first communication shows that of the causes therein examined, the most potent in affecting the latency are variations in temperature and fatigue; of secondary importance are the strength of stimulation and the mode of suspension of the extending weight.

Temperature.—In the gastrocnemius of an "April frog" (indirect stimulation) we saw for an excursion through 20° C. (viz., from 5° to 25°) a variation of ·014″ in the length of the latency; in the muscle of another animal heated from the normal room temperature (17°) through 14° C., a variation of ·01″ was obtained. Taking the room temperature as the starting point, we find in these experiments that lowering the temperature through 5° increased the latency ·004″, ·0033″, and ·0027″ respectively. Heating through 5° above the normal yielded a shortening of ·0016″—·0012″, but though these figures represent a usual result, occasionally there is a much more extensive variation. Thus, in one case with an unusually long latency (·017″) at the room temperature, heating through 5° reduced the latency ·01″. After this point in the heating process had been reached, the course of the latency under higher temperatures was strictly comparable with that of other muscles with a more ordinary initial latency, and we should regard this circumstance as furnishing a proof that this abnormally long latency was in reality owing to

some unstable cause not usually operative. We have seen such muscles allowed again to cool to the room temperature fail to give again the long initial latency at first manifested, whereas, as a rule, the result obtained from a given temperature for the same muscle is constant or nearly so, should heating and cooling not have been carried to a deleterious extent. We cannot regard a muscle, showing a long latency and a long curve, as being in both respects in series with a more quickly contracting muscle, cooled down through a certain range of temperature. One of the most important features in the divergence, is in the change of elasticity in the case of the cold muscle, but beyond this we have variations of kind between muscles which must help to account for the intimate relationship between the latency and curve in any given muscle.

Fatigue.—M. Ranvier has recorded the remarkable fact that the latency of the thoroughly fatigued red muscle of the rabbit, may bear the proportion to that of the fresh muscle of nearly five to one. He says, if the strength of the stimulation is increased, the latency shortens again, as contractibility is redeveloped. Since the fatigued muscle is equally elastic, but less irritable than the fresh muscle, a stimulation which at first produces a maximal result, soon becomes sub-maximal, then minimal, and finally ceases to be effective; so that constant increase of stimulation is required to elicit an equal (in the sense of a maximal) effect. Mendelssohn has described an increase of latency from ·008″ to ·03″ in the gastrocnemius of the frog as the result of fatigue. These extensive variations are quite possible, but it not infrequently happens that the length of the latency is rather apparent than actual as a result of fatigue. A careful examination of the curve of a fatigued muscle will often enable us to determine a very gradual but definite departure of the lever attached to the muscle from the abscissa, in what, at first sight, seemed to be the actual latency. This would be concealed by a thick abscissa, or lost by the use of a too slightly amplifying lever.

In our former paper we gave tables showing that 1,300 induction shocks (producing maximal single contractions), increased the latency ·00526″, and that two minutes' tetanus had the effect of lengthening this period ·0066″. We also pointed out that it is in the extreme of fatigue that the rapid increase in the latency occurs. Exercise short of distinct fatigue was seen even to shorten the latency to a slight extent. This may have been in part due to the increase of extensibility which Volkmann has shown occurs in earlier stages of fatigue of the muscle. In the later stages of fatigue, however, the extensibility decreases as the elasticity of the shortened muscle increases, and here we have a corresponding *increase* in the latency.

The effects of variations of strength of stimulation and in the amount of weight employed, and the manner of employing it, have

been discussed in our previous paper, and need not occupy us here; from a physiological point of consideration these are in the economy of the living animal liable to smaller variations, and therefore of less interest than the effect of change of temperature and fatigue.

Physiologically considered, the weight raised when the muscle is in service will be constant for the individual, when the stimulations are equal. The researches of Navalachin have shown that most work is done and less fatigue produced when stimulation sub-maximal in character is applied to the frog's muscle, and no doubt the muscle in service during life is usually excited by sub-maximal stimulation (in an electrical sense). It is important to bear in mind that a constant weight used in a series of experiments bears a different relationship to the muscle of a frog weighing x grms. or x + or x − grms., inasmuch as it affects variously the elasticity of the stronger or weaker muscle. In highly extensible parallel-fibred muscles with a small limit of elasticity, such as the hyoglossus, the divergencies obtained by incommensurate weightings are very considerable.

Our experiments tend, we think, to support the idea which has been expressed by many physiologists, that the relationship between length of latency and the conditions of elasticity and extensibility of the muscle is a close one.

Conclusions.

1. The limits within which the normal latency varies (intentionally introduced extrinsic influences apart) appear to be as follows:—

a. In gastrocnemii of various frogs at different seasons—

Rana temp. ·008″—·0208.″

b. In different muscles of the same animal—

Frog ..	·008″ (gastrocnemius)	to	·022″ (hyoglossus).
Toad ..	·012″ (triceps)	,,	·024″ (hyoglossus).
Tortoise	·022″ (omohyoid)	,,	·036″ (ext. dig. com., &c.).

(The complete exclusion of certain influences, nutritive, thermal, &c., is impossible.)

2. Conclusions as to the length of the latent period based on the duration of the contraction are liable to error; especially is this the case when we attempt to reason for one class of animals from the relationship found in another.

3. The duration of the latency increases and decreases in direct but unequal proportion to the amount of weight which the muscle has to lift.

4. Increase in strength of stimulation is accompanied by a shortening of the latent period. The variation seems to depend on the absolute strength of the stimulus employed, viz.: (*a*) Increase from minimal to stimulation giving rise to maximal contraction is accom-

panied by a steady and marked decrease in the duration of the latency. (*b*) When once maximal contractions are arrived at, considerable increase in strength of stimulation does not alter the length of the latency. (*c*) After a certain point has been reached, further increase in strength of stimulus (hyper-maximal) causes elongation of the latent period associated with signs of injury to the tissue.

5. Fatigue must attain a considerable degree before it materially affects the length of the latency. When it once begins to produce an effect it rapidly lengthens the latent period of muscles removed from the animal or in which circulation has ceased.

6. Changes in temperature, even minimal in amount, cause a marked alteration in the latency.

Lowering of temperature is accompanied by a steady elongation, and elevation by a rapid shortening of the latent period. When the heat becomes intense (for frog over *circa* 36° C.) the length of the latency seems again to increase, as the muscle passes into heat rigor.

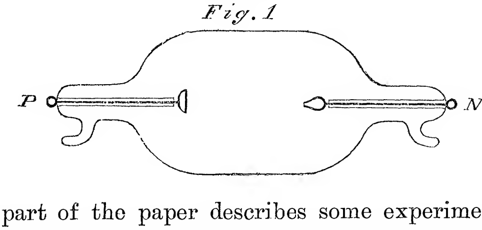
7. In observing the above variations in the duration of the latency, we have failed to find the wide extremes given by some authors as the limits of this phase of the contraction of striated muscle

V. "Experimental Researches on the Electric Discharge with the Chloride of Silver Battery. Part IV." By Warren De La Rue, M.A., D.C.L., F.R.S., and Hugo W. Müller, Ph.D., F.R.S. Received June 11, 1883.

(Abstract.)

The authors recall that at the conclusion of the third part of their researches,* they stated that they intended to make an investigation on the dark discharge, and the special conditions of the negative discharge; this paper contains a number of experiments, more especially on the latter subject, and also others intended to throw light on the general nature of the electric discharge through gases.

Fig. 1



The first part of the paper describes some experiments made with vessels of different forms in order to ascertain whether the dimensions

* "Phil. Trans." vol. 171, p. 65.